Tilefish, *Lopholatilus chamaeleonticeps*, habitat, behavior and community structure in Mid-Atlantic and southern New England waters

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Synopsis

We made forty-one submersible dives along the outer continental shelf in the Mid-Atlantic-southern New England region to study tilefish distribution, abundance, habitat and behavior, and the structure of the community associated with tilefish habitats. Tilefish are shelter seeking and inhabit three more or less distinct habitats: (1) horizontal excavations in clay outcrops along the walls of submarine canyons (pueblo habitats); (2) scour depressions under rocks and boulders and; (3) the primary habitat, funnel-shaped vertical burrows in horizontal clay substrates. There appear to be two critical habitat requirements, relatively warm (9–14° C) stable bottom temperatures and the availability of shelter or a malleable sustrate in which to construct a shelter. Suitable substrate for burrowing is usually provided by clay that is frequently exposed around submarine canyons. At least some vertical burrows were seen at most dive locations within the study area except at Norfolk Canyon. Pueblo and boulder habitats were mostly associated with submarine canyons off New England, and excavations under rock slabs were occupied in Baltimore Canyon. Vertical burrows occurred from 80–305 m, but where vertical burrow and other habitats co-occurred, burrows were in shallower water (<120 m). Vertical burrows were contagiously distributed, and significantly larger and more dense at the Mid-Atlantic dive sites than off New England (mean diameter and density = 1.6 m and 1234 per km² at Hudson Canyon, 0.88 m and 624 per km² at Veatch Canyon and 0.88 m and 145 per km² at Lydonia Canyon). Various crustaceans (e.g. *Munida* spp., *Cancer* sp., and goneplacid crabs) and fishes (e.g. *Conger oceanicus, Anthias* spp., *Urophycis* sp. and *Helicolenus dactylopterus*) were more abundant in than away from burrows. Many species either live in or around the tilefish burrow so that the upper margin of the burrow is honey-combed by their secondary burrowing. We believe burrows are formed by a combination of oral excavation by tilefish, secondary bioerosion by associated species, and tilefish swimming motions to flush fine sediment from the burrow. Tilefish appeared to orient to particular vertical burrows, and time lapse photography showed that fish may pair in burrows. Noncorresponding, temporal activity patterns of tilefish and associated species may indicate that predation by tilefish is a strong organizing principle in the community associated with tilefish burrows.

Introduction

Since 1972 an important fishery for tilefish (*Lopholatilus chamaeleonticeps* Goode and Bean) has developed along the edge of the continental shelf in the Mid Atlantic – southern New England region. Concern over management of this resource and possible conflicts with offshore oil drilling has

prompted our studies of tilefish habitat, behavior and community structure. Tilefish are known to occur from Nova Scotia (Markle et al. 1980) to Surinam (Dooley 1980), excluding the Caribbean Sea. In North American waters two stocks are recognized, one found north of Cape Hatteras and a second in the South Atlantic Bight and Gulf of Mexico (Katz et al. 1982). This paper considers the northern stock. Observations from submersibles to date have shown that tilefish inhabit pueblo habitats in clay outcrops along the walls of submarine canyons (Cooper & Uzmann 1977, Warme et al. 1977) and scour depressions around large boulders (Valentine et al. 1980) in the southern New England region. They also occupy vertical burrows in clay substrate around Hudson Canyon (Able et al. 1982). This paper adds to the knowledge of tilefish habitats, behavior and community structure in the Mid Atlantic-southern New England region. In particular, we more completely describe the physical nature of the habitats, and indicate their distribution and abundance. Furthermore, we discuss the interrelationship of physicochemical factors that correlate with the distribution of the tilefish, and consider the structure and organization of tilefish communities.

Materials and methods

A series of submersible cruises were conducted along the east coast of the U.S. (Fig. 1) during late July to mid August of 1980–1984 (Table 1). All dives reported here were conducted with the four-man submsersible *Johnson-Sea-Link* and its support ship R/V *Johnson* from Harbor Branch Foundation. This submersible has two manned compartments, the forward one, consisting of an acrylic sphere, houses the pilot and one observer. The aft compartment is constructed of aluminum and has large flat observation portholes both port and starboard. This compartment is manned by a tender and another observer.

Generally dives were made either along straight line transects (across or along depth contours) or in accordion shaped tracks (see mapping below). On other dives the submersible moved very little when specific tasks (behavior observations, burrow measurement and dissection, etc.) were planned. During a typical dive, physical (bottom temperature, depth, topography, visibility, current speed and direction and substrate type) and biological (tilefish abundance, size, sex, behavior, burrow number and dimensions, and associated fish and macroinvertebrates) parameters were recorded on audio tapes. Photographs were taken with one or

Table 1. Summary of submersible operations for tilefish studies along the east coast of the U.S. during 1980–84. See Figure 1 for locations. Major locations include Lydonia (LC), Veatch (VC) and Hudson (HC) canyons. Habitat types indicated as vertical burrow (VB), pueblo habitat (PH), boulder field (BF) or other (OH, see text for explanation).

| Year	Location (Canyon)	Cruise dates	Number of dives	Depth range of observations	Types of habitats observed
1980	Lydonia	6–18 August	12	LC = 139–192 m	LC = VB, PH, BF
	Veatch			VC = 117–229 m	VC = VB, PH, BF
	Hudson			HC = 146–156 m	HC = VB
1981	Lydonia	23–28 July	12	LC = 134–268 m	same as 1980
	Veatch			VC = 122–213 m	
	Hudson			HC = 144–241 m	
1982	Hudson	22–30 July	9	129–227 m	VB
1983	Hudson	15–16 August	4	119–175 m	VB
1983	Baltimore	17 Aug	2	204–253 m	OH, BF
1983	Norfolk	18 Aug	2	175–247 m	OH
1984	Middle Grounds	29 Jul–3 Aug	10	102–243 m	VB
1984	Atlantis	29 Jul–3 Aug	2	183–337 m	VB
1984	Veatch	4 Aug	1	130–132 m	VB
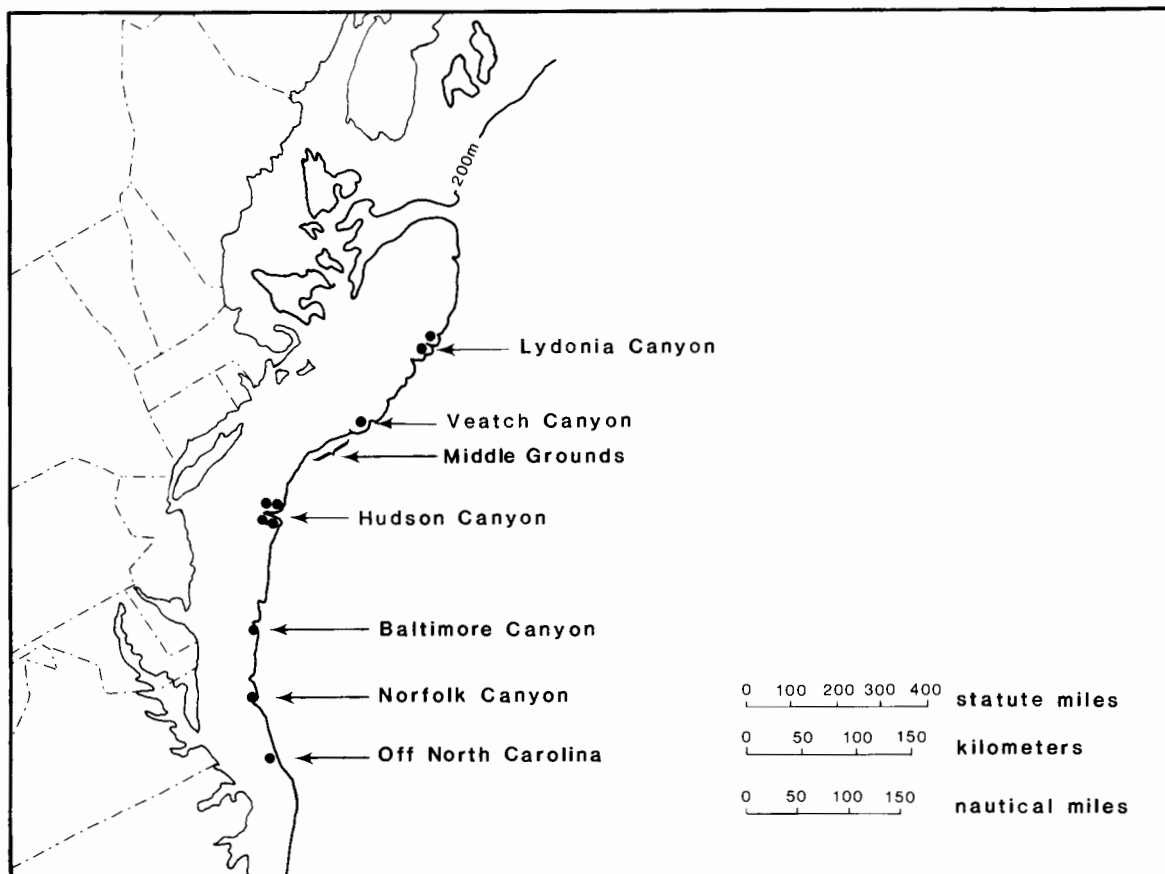
Fig. 1. Map of U.S. east coast showing study sites.

two externally mounted 35 mm cameras and a bow-mounted video camera. Correlation of 35 mm photographs with audio tape records was facilitated by a time-date record exposed on each 35 mm frame.

Estimates of tilefish length, habitat dimensions and densities of associated fish and macro-invertebrates were made from 35 mm photographs projected onto grids of known dimensions. The grids were originally photographed with the submersible ashore. Estimates for the above measurements were then corrected to reflect the differences in light transmission from air to water. These estimates were validated with in situ measurements of objects from *Johnson-Sea-Link* using rods and weighted lines marked in known increments and checked against photographic estimates of the same objects. Density estimates for tilefish and burrow abundance were determined using the

numbers of fish and habitats seen, the length of the submersible transects and the width observed along the tracks (based on visibility estimates by the submersible pilot and the observer). Interpretation and description of habitat types, tilefish behavior, etc., were aided by reviewing video tapes made during the dives.

Tilefish habitat distribution, including distance between burrows, was determined by mapping small discrete areas in the vicinity of Veatch, Lydonia and Hudson canyons. On these dives, the transects followed an accordion-shaped pattern over the sea floor. The pattern usually consisted of six legs, each 366 m in length and run parallel with one another. Intervals of 91 m connected the end of each leg with the beginning of the next leg. The pilot kept the submersible on track using an onboard gyro compass and doppler sonar. The dop-

pler unit not only helped keep the submersible on course but also provided a record of distance traveled. The R/V *Johnson* followed the submersible with a short baseline acoustic tracking system and the data were recorded on a Loran C plotter.

During mapping dives burrow counts were made by the forward observer and confirmed by the aft observer when possible. The total distance traveled, including distance between burrows, was read from the doppler sonar and noted along with depth each time a burrow was recorded.

We collected small organisms and made additional observations using equipment unique to *Johnson-Sea-Link*. Fishes and macro-invertebrates associated with tilefish habitats were poisoned by injecting a rotenone solution directly into burrows, and then sucked into an ambient pressure collecting box through a nozzle attached to the end of the manipulator arm. Tilefish burrows were dissected with the jaws of the manipulator arm or by blowing burrow sediments away with the submersible bow thruster.

A single tilefish habitat, studied intensively in Lydonia Canyon in 1980, was revisited in 1981 using the Loran C navigation on the R/V *Johnson* and known coordinates of a pinger deployed by the National Marine Fisheries Service the previous year.

A 35 mm camera and strobe, controlled by an intervalometer, were mounted on a tripod and used to take time-lapse photographs of tilefish and their burrows. The camera system was deployed at a vertical burrow near Hudson Canyon in 1982 by *Johnson-Sea-Link*, and photographs were taken every 2.0 min over a 24 h period.

Results and discussion

Observations from submersibles (Table 1) have shown that tilefish are shelter seeking fishes that occupy a variety of habitats. We currently recognize three more or less distinct types along the northeast coast of the U.S.A.: rocks and boulders,

pueblo habitats and vertical burrows (Fig. 2). Although these habitats have certain characteristics in common (e.g. bottom water temperature), the occurrence and utilization of the different habitats varies with geological setting, latitude and season.
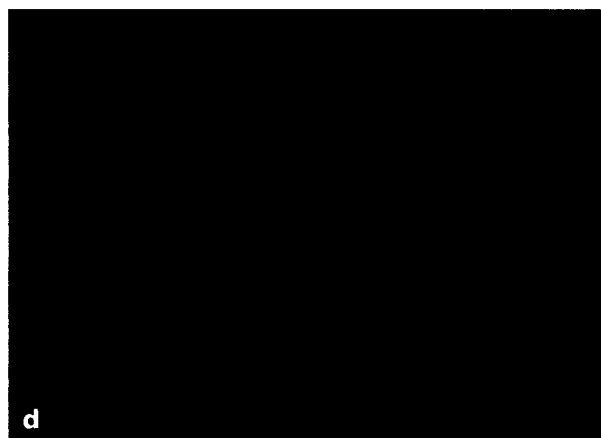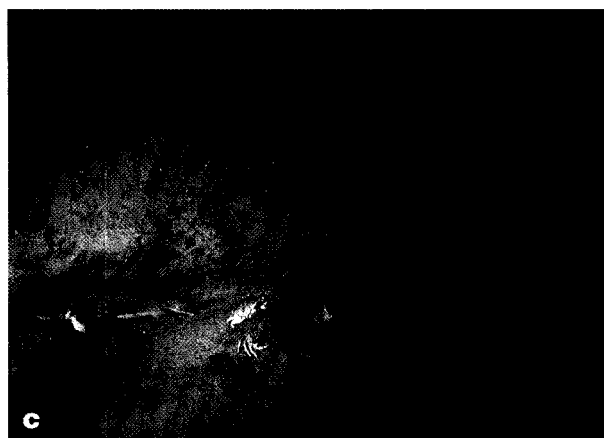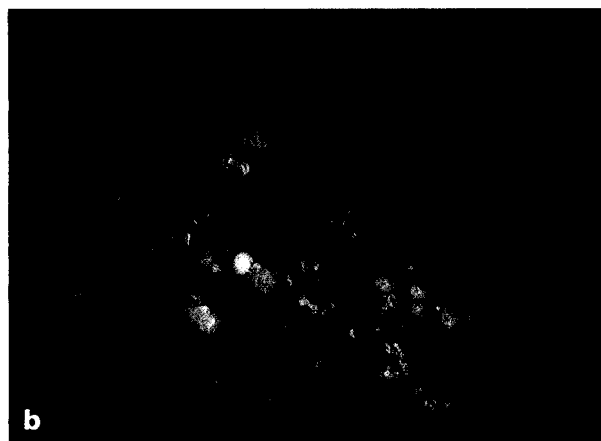
Boulders and rocks

The association of tilefish with large boulders was the simplest type of habitat we observed (Fig. 2a). The boulders, either singly or in clumps, were observed on the rims and along the walls of submarine canyons. Boulders appeared to be placed randomly, as would be expected if they are the result of glacial rafting (Valentine et al. 1980). At dive sites in Veatch and Lydonia canyons, boulders were often interspersed with pueblo habitats along canyon walls. The boulders were variable in size and shape and ranged from 0.3–5 m in diameter. As described by Valentine et al. (1980), boulders were often in shallow scour basins. Scouring is probably of combined physical and biological origin.

Tilefish were observed utilizing this habitat in depths of 149–242 m in Veatch, Lydonia, Hudson and Baltimore canyons; and in Oceanographer Canyon (Valentine et al. 1980). Boulders occupied by tilefish were seen very infrequently at Hudson and Baltimore canyons (once and three times, respectively), but many times at Veatch and Lydonia canyons. Thus, this habitat appears to be most common in the New England area which was closer to the late Pleistocene glaciers, the source of these boulders (Valentine et al. 1980).

Tilefish evidently use boulders for shelter. Typically, tilefish rested motionless against or, if possible, under a portion of a boulder. In most instances a single adult tilefish was observed at each boulder, but on occasion three could be seen simultaneously.

The utilization of boulder habitats may be random and temporary. On several occasions we chased tilefish away from boulders with the submersible and followed them to note their subsequent choice of habitats. In every instance the

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Fig. 2. 35 mm photographs of tilefish habitats. *a* – boulder field; *b* – rock slab in anemone fields; *c* – pueblo habitat; *d* – tilefish grottos at Norfolk Canyon; *e* – vertical burrow at Hudson Canyon; *f* –vertical burrow at Lydonia Canyon.

tilefish stopped at other boulders and then moved on, and showed no tendency to return to the original boulder. Choice of a boulder appeared random, and not related to boulder shape or size nor residency by other tilefish.

We observed four tilefish occupying excavations under rock slabs (Fig. 2b) among anemone fields at a dive site along the southwest wall of Baltimore Canyon (Lat 38° 09′ 31″ N, Long 73° 52′ 02″ W). Numerous rock slabs, about 1 by 2 m, lying at varying angles to the slope covered the bottom for a distance of over 150 m on a steeply sloping (estimated 30°) canyon wall from 204 to 253 m depth. Excavations in the grey sediment under and adjacent to rocks were common and appeared to be of biological origin. The larger excavations were inhabited by tilefish. Fish appeared to be residents of these habitats, because they would not leave their habitat when prodded with the manipulator arm of the submarine, as they did at boulder habitats.

Certain crustaceans and fishes were commonly associated with rock and boulder habitats (Table 2). Most of these associates were found with tilefish in all habitats, except for *Macrozoarces americanus* and *Brosme brosme,* which were only observed at southern New England sites, and *Sebastes* sp. which was only seen at Baltimore and Norfolk canyons.

Pueblo habitats

These habitats have been illustrated and described (Warme et al. 1977) as a relatively localized area of submarine canyon wall where megabenthic crustaceans and finfish have intensively bioeroded depressions and borings into the substrate and have occupied these sites. We observed, as did Warme et al. (1977) and Valentine et al. (1980), that pueblo habitats always occurred in the stiff grey clay found as outcrops along the walls of submarine canyons (Fig. 2c). The excavations occupied by tilefish were dug horizontally into the canyon wall, and were variable in shape and size. The smallest were just large enough to admit the girth of the tilefish, while

Table 2. Fishes and crustaceans observed at various tilefish habitats along northeast coast of the U.S. during 1980–84. Each species was observed every year (see Table 1) unless noted, HC = Hudson Canyon, VC = Veatch Canyon, LC = Lydonia Canyon, BC = Baltimore Canyon, NC = Norfolk Canyon and MG = Middle Grounds.

Species	Boulders and rocks	Pueblo habitats	Vertical burrows
Crustaceans			
Munida spp.[a]	VC, LC	VC, LC	VC, LC
Munida longipes	BC	NC	–
Cancer sp.	VC, LC	VC, LC	VC, LC, HC
Acanthocarpus alexandri	–	–	HC
Homarus americanus	VC, LC	VC, LC	VC, LC, HC
Bathynectes longispina	BC	NC	HC
Chacellus filiformis	–	–	VC, HC
Tridentella recava[b]			MG
Fishes			
Conger oceanicus	VC, LC	VC, LC	VC, HC
Macrozoarces americanus	VC, LC	VC, LC	–
Brosme brosme	VC, LC	–	–
Anthias spp.	VC, LC, BC	VC, LC, NC	VC, LC, HC
Helicolenus dactylopterus	VC, LC, BC	VC, LC, NC	VC, LC, HC
Sebastes sp.	VC	NC	–
Urophycis sp.	–	VC	HC
Laemonema sp.[c]	–	NC	–

[a] Three species have been identified from collected specimens, *M. iris*, *M. valida* and *M. forceps*. However, it is not possible to distinguish them from submersible sightings or photographs.
[b] A new isopod species (T.C. Bowman 1986).
[c] Provisionally identified as *L. barbatum*.

others were as much as 1 m wide by 3 m long and 1 m deep. They often had multiple openings into a single large space (grotto). Large openings often angled down inside the entrance. Outside the grotto opening there was often a horizontal sediment terrace. The sediment of the terrace appeared identical to that inside the grotto and was probably transported there during excavation. Dissections of a pueblo habitat (Veatch Canyon) with the mechanical arm of the submersible revealed that the smaller secondary burrows (type two of Warme et al. 1977) do not penetrate very deeply into the substrate. When the underlying substrate was exposed it was usually darker than the surface sediment, suggesting a reducing environment. Dye marker experiments (rotenone which becomes opaque in sea water) revealed that the smaller openings into the grotto from the substrate surface were common and numerous. These small secondary burrows were occupied, and presumably constructed, by galatheid and cancrid crabs.

Pueblo habitats, occupied by tilefish, were commonly observed in Lydonia, Veatch (the latter also by Warme et al. 1977) and Oceanographer canyons (Valentine et al. 1980). During our dives these habitats were found from 170 to 245 m depth. We have never observed pueblo habitats in Hudson Canyon, even though we have made many more dives there (Table 1).

The behavior of tilefish occupying pueblo habitats was similar to the behavior of fish under rock slabs, but different from fish associated with boulders. When approached by the submersible, tilefish always entered head first, and then usually pressed themselves against the back of the grotto and remained motionless. When several tilefish occupied the same grotto, they usually pressed against each other and remained passive. Exits from the grotto were either tail first or head first. The latter was possible because there was frequently sufficient room for the fish to turn around in the grotto. After acclimation to the presence of the submersible, tilefish would leave the grotto but remained in the immediate vicinity (within 2–3 m). At this time they hovered nearby, usually laterally to the submersible, while slowly sculling with the pectoral fins. If disturbed, they moved directly back into the grotto and became motionless once again.

Individual tilefish may be long-term residents of the same pueblo habitat. In 1980, three different tilefish were observed and photographed in a pueblo habitat in Lydonia Canyon. Two observers independently identified the three fish on two dives using size, body scars and pre-dorsal flap size. We returned to this pueblo habitat approximately one year later in 1981, and two of the tilefish observed in 1980 were still present. We recognized these fish from distinctive body scars observed both first hand and on video tape.

Striking changes had taken place in this pueblo habitat in one year, attesting to the significant erosional capabilities of tilefish and their associated species. We easily recognized the site by the overall shape of the grotto, the number and location of smaller burrows around the periphery and the location of specific cobbles in and around the grotto. The width of the grotto had increased by approximately 60–80 cm (to 1.5 m wide by 0.5 m at the greatest height) because of the collapse of a column of clay between an adjacent burrow and the main grotto opening. Pieces of the column (largest approximately 25 cm) were still present at the former location of the column. A review of videotapes and 35 mm photographs from all dives at this site indicated that the smaller burrow had been connected to the back of the grotto and apparently the tunnel was widened until the clay column separating the two collapsed.

In both years the inhabitants of these larger adjacent burrows (25–55 cm) were *Conger oceanicus, Macrozoarces americanus* and *Cancer* crabs. In one instance a *Conger oceanicus* disappeared from one of the adjacent burrows and reappeared in the grotto, indicating that they were interconnected. Interconnecting of the chambers in the habitat probably increases instability and promotes cave-ins, resulting in marked changes over time (e.g., as described in preceding paragraph).

Tilefish habitat that was very similar to pueblo habitat was observed along the north wall of Norfolk Canyon between 175 and 247 m (Fig. 2d). This habitat also consisted of extensively bioeroded areas of stiff grey clay. However, the habitat was

topographically complex with several large clay blocks thrust up above the surrounding substrate, with vertical walls and overhangs 25 m high. One grotto was about 2 m across. Tilefish inhabited the largest of the grotto-like excavations. These grottos tended to be directed perpendicular to the plane of the wall, i.e., horizontal into near vertical walls and angled toward the vertical into more gently sloping walls.

We noted large piles of angular clay debris at the base of the steep clay walls, probably indicating that the community is periodically disturbed by spalling off of clay. Presumably animal burrowing weakens the surface of the clay walls and they eventually collapse under the force of gravity, falling off in sheets.

Although these Norfolk Canyon habitats were physically very similar to pueblo habitats, they were quite different biologically (Table 2). The community in Norfolk Canyon was characterized by presence of numerous anemones (*Halcurias pilatus*) living attached to the burrowed clay. *Anthias* sp. (Table 2) was common, along with *Sebastes* sp., the galatheid crab *Munida longipes* and the portunid crab *Bathynectes longispina*.

Vertical burrows

Structure
We believe vertical burrows are the primary habitat of tilefish in the Mid-Atlantic and southern New England area. Able et al. (1982) described and estimated the dimensions of vertical burrows occupied by tilefish near Hudson Canyon that were funnel-shaped and extensively secondarily burrowed along the upper margins (Fig. 2e). Actual measurements were mean depth = 1.7 m (range = 1.25–2.3 m, n = 6) and mean upper cone diameter = 1.6 m (range = 0.3–3.5 m, n = 51). Very large burrows (estimated up to 5 m in diameter) could not be measured because they were too large to be entirely within the photographic field of view. Even larger diameter U-shaped features (estimated up to 9–10 m across) were observed. They were secondarily eroded like funnel-shaped burrows, but with as many as three individual burrow shafts cut into their lower portions.

Several experiments we performed allow us to describe the structure of burrows more fully, and better understand how burrows are formed. We used the bow thruster of the submersible to wash away fine silty sediments from the substrate outside (but near) a burrow margin and discovered that secondary bioerosion was absent. This indicates that secondary burrows are not relict features in the Pleistocene clay that are covered by recent fine sediments and exposed only in tilefish burrows.

By injecting a dye marker into burrows we determined that the larger secondary burrows located at the burrow margin were interconnected to the main burrow shaft (Fig. 2e). Goneplacid crabs were collected as they emerged from these secondary burrows.

Smaller secondary burrows around the burrow margin were occupied by galatheid crabs (Able et al. 1982), and we determined that these burrows do not penetrate deeply into the substrate.

Using the grab sampler on the submersible manipulator arm we collected large pieces of clay relatively intact from several burrow margins. Dissection of this clay revealed fine scale secondary erosion of burrows. These smallest secondary burrows discovered in the clay were apparently occupied and constructed by two crustaceans. Burrows 2–5 mm in diameter had distinct fine curved sculpting along the walls, and were occupied by *Tridentella recava* (Table 2). Other, slightly larger, secondary burrows (8–10 mm diameter) were unoccupied, but the walls of the burrow had a distinct straight, coarser scale sculpting than the isopod burrows. The coarser scale and fewer excavation marks suggests that these burrows were probably constructed by crustaceans with fewer appendages, most likely goneplacid crabs.

The interconnected structure of burrows provides a means for passive ventilation of the tilefish burrow system. Because interconnected secondary burrow openings are at the burrow margin near the surrounding substrate, and the main tilefish burrow shaft is at the bottom of the cone, the secondary openings are more exposed to any uni-directional fluid flow (and we have recorded currents up to one knot from the submersible). Pressure differences at burrow apertures could be generated by

variations in fluid velocity along a streamline (i.e. Bernoulli's principle), thus inducing flow down the large central burrow and out the smaller secondary holes (Okubo 1980). A second mechanism, 'viscous sucking', or the tendency for fluid to leave the opening exposed to highest external velocity and enter the other end (Okubo 1980), could also play a role. However, as pointed out by Okubo (1980), a larger hole usually provides a better exit than a small hole. In any case, active burrow ventilation by tilefish may be equally or more important than passive ventilation, because we have often observed clouds of fine sediment being moved out of the central burrow presumably by tilefish swimming motions.

Able et al. (1982) reported shallow depressions with smooth silt covered bottoms and little or no secondary bioerosion at the margin, which were interpreted to be abandoned burrows. We have observed abandoned burrows with increasing frequency since 1979; no doubt this has resulted from the continued expansion of the tilefish commercial longline fishery which reduced the population size by about one-half to one-third from 1979 to 1982 (Turner et al. 1983).[2]

Spatial distribution

Tilefish burrows are contagiously distributed. We compiled the frequency distributions of distances between all adjacent burrows observed along submersible transects (Fig. 3). In the Hudson Canyon area 27% of burrows were less than 20 m apart. The ratio of the variance to the mean distance between burrows (index of dispersion, I; Pielou 1977) was much greater than unity for both Hudson and Veatch canyons (I = 86.1, n = 384; I = 143.4, n = 103). Burrow distribution was therefore concluded to be contagious. Twichell et al. (1986) have suggested that tilefish bioerosion (i.e. the burrowing of contagiously distributed tilefish over the past 13 thousand years) may have played an important
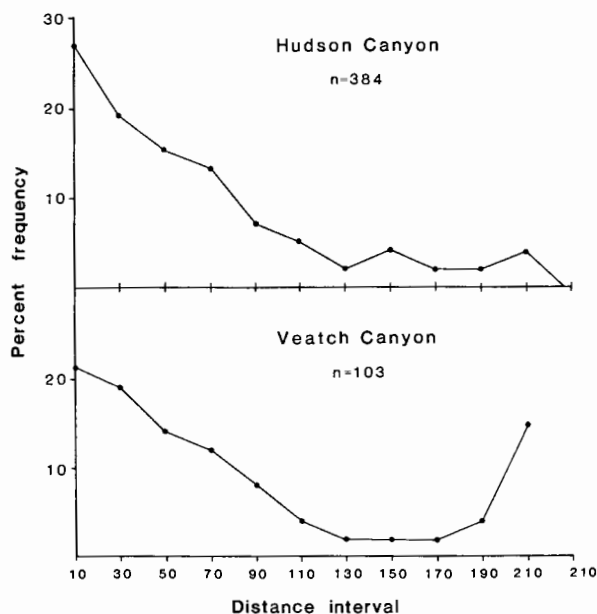
[2] Turner, S.C., C.B. Grimes & K.W. Able. 1983. Report to the Mid-Atlantic Fishery Management Council on the Rutgers University preliminary tilefish stock assessment. Unpublished report, 22 pp.

Fig. 3. Frequency polygons of distances (in m) between adjacent burrows along submersible transects for Hudson and Veatch canyons.

role in shaping bottom topography around Hudson Canyon.

Origin and age

Able et al. (1982) hypothesized that the upper conical portion of large burrows was formed through the combined activity of tilefish and galatheid crabs. Galatheids, which inhabit the upper conical portions of burrows, were proposed to displace sediments into burrows. In turn, these sediments are forced out by tilefish swimming movements, eventually resulting in the characteristic conical upper margins of large burrows. Goneplacid crabs and isopods may also displace sediment into the burrows. Perhaps more importantly, the discovery that some secondary burrows interconnect to the main burrow indicates that the upper portion of some burrows is 'honey combed' and prone to eventually collapse. This is probably an additional mechanism involved in the formation of conically shaped burrows.

Oral excavation by tilefish may be another means of burrow construction. We have observed clay clumps near occupied burrows that were the correct size and shape to be mouthfuls of sediment

removed by tilefish. Resuspension by water movements and bioerosion by associated species probably both act to breakdown and change the shape of these clay clumps so that they quickly become unrecognizable.

These mechanisms explain the origin of funnel-shaped burrows, but do not account for the larger diameter (estimated up to 9–10 m) crater-like features that we observed. These U-shaped features probably formed by the coalescence of closely spaced vertical burrows.

We do not know how long it takes to construct a burrow, or if more than one generation is involved. Large burrows could be quite old if they have been successively occupied by generations of tilefish. This is because individual tilefish live in excess of 30 years (Turner et al. 1983), and the clay that burrows are dug into is Pleistocene deltaic sediment that was deposited 12–14 thousand years ago (D.C. Twichell, personal communication).

Even though a burrow might be old if continuously occupied, they fill in rapidly when abandoned. We rotenoned, netted and removed the tilefish from a 2 m diameter burrow near Hudson Canyon in 1982, then marked the site with an acoustic transponder and revisited the same burrow in 1983. The burrow was not re-occupied and was almost totally silted in. This suggests that an abandoned burrow would fill with sediment in at most one year, or perhaps less, because we do not know if the burrow was occupied during the period between removal of the tilefish in 1982 and our revisit in 1983. This rapid fill-in rate shows that burrows require considerable maintenance, and may suggest that fish mostly dig their own burrows (as opposed to occupying an existing one) because juveniles would probably not be able to maintain a large burrow.

Associated species

Species that are sparse over open bottom are concentrated in and around burrows, forming a definite tilefish community (Table 2). Several additional species (not recorded by Able et al. 1982), were observed in close association with burrows (the crabs *Chacellus filiformis* and *Munida longipes*, and the isopod *Tridentella recava*; the fishes

Anthias spp., and *Urophycis* sp.; Table 2). The two fish species were observed inhabiting the larger secondary excavations in the lower portion of the burrow cone. Both species were cryptic and seen only in rotenoned burrows. Able et al. (1982) suggested that associated species appeared more numerous in and around burrows, and actual counts of some associated species in photographs at and away from (but nearby) burrows confirm this (Table 3). Approximately 60–80% of the galatheid crabs, cancrid crabs and blackbellied rosefish counted were associated with burrows at all canyons. However, only galatheid crabs were statistically more abundant (p<0.05) near burrows, particularly when the data were partitioned by specific submarine canyon (Table 3). These data give the misleading impression that all three species were rare (mean abundance less than one per burrow). This is because counts were made from photographs taken by a camera mounted at a fixed angle approximately 3 m off the bottom. Therefore, we could not obtain the best possible photographic angle of a burrow. Also, the data were averaged across many burrows of various sizes, including many small burrows which typically had few or no associates. Counts obtained from the time lapse photography yielded more realistic abundance data. At times of peak abundance, as many as 25 galatheids, 5 goneplacids, 1 *Anthias* sp., 1 *Urophycis* sp. and 1 *Helicolenus dactylopterus* were photographed at a single large (2 m diameter) burrow (Fig. 4).

Several factors may account for greater abundance of associated species near burrows. Some species are shelter seeking and associate with structures that provide protection (presumably from predation). For example, galatheid crabs and *H. dactylopterus* are also seen associated with shells, cobbles and cerianthid anemone pedal disks, all of which afford some shelter. Galatheid and goneplacid crabs are both burrowers (facultative, and perhaps obligatory in the latter case, because we have only observed goneplacids in secondary burrows) and probably require a malleable substrate such as exposed clay to burrow in. Also, it could be difficult for them to maintain burrows on open bottom with no tilefish to maintain the burrow and

Table 3. Results of t-test of differing abundance of galatheid crabs, cancrid crabs and *Helicolenus dactylopterus* in and away from tilefish habitats near three Mid Atlantic-southern New England submarine canyons in 1980 and 1981. B = in burrow, A = away; habitats at Hudson and Veatch canyons were vertical burrows, but Lydonia Canyon habitats were pueblo habitats and boulder fields (*significant at 0.05 level).

Location	Proximity to habitat	Number photos analyzed	Number crabs counted	Mean crabs per photo	t-value	Conclusion
			Galatheid crabs			
Hudson	B	60	45	0.75	2.463*	$0.02 > p > 0.01$
Canyon	A	60	14	0.23		
Veatch	B	60	7	0.12	1.572	$0.2 > p > 0.1$
Canyon	A	60	2	0.03		
Lydonia	B	60	82	1.37	4.37*	$p > 0.001$
Canyon	A	60	18	0.30		
All canyons	B	180	134	0.74	4.65*	$p > 0.001$
	A	180	34	0.19		
			Cancer sp.			
Hudson	B	60	12	0.20	1.897	$0.1 > p > 0.05$
Canyon	A	60	5	0.08		
Veatch	B	60	9	0.15	1.20	$0.4 > p > 0.2$
Canyon	A	60	5	0.08		
Lydonia	B	60	0	0.00	3.134*	$0.05 > p > 0.001$
Canyon	A	60	4	0.07		
All canyons	B	180	21	0.117	1.30	$0.2 > p > 0.1$
	A	180	14	0.077		
			Helicolenus dactylopterus			
Hudson	B	60	3	0.05	1.132	$0.4 > p > 0.2$
Canyon	A	60	1	0.02		
Veatch	B	60	4	0.07	3.134*	$0.005 > p > 0.001$
Canyon	A	60	0	0.00		
Lydonia	B	60	0	0.00	2.33*	$0.05 > p > 0.02$
Canyon	A	60	2	0.03		
All canyons	B	180	7	0.04	1.27	$0.4 > p > 0.2$
	A	180	3	0.02		

remove fine silty sediments that would otherwise fill in their small burrows. Therefore, mobile associated species may actually immigrate to burrows, or if most species of associates settle at random from the plankton, higher mortality away from burrows could result in greater abundance in burrows.

There could also be trophic rewards for being associated with burrows. Tilefish feeding and excretion may make the burrow a more food resource rich environment for associates. Regardless of the nature of the benefits of association with burrows, the advantages gained must exceed the disadvantages of danger from predation, because some as-

sociates (in particular galatheid and cancrid crabs, and probably *H. dactylopterus* are components of the diet of tilefish (Turner & Freeman, unpublished).[3]

Time lapse photography also revealed distinct activity patterns for some associated species in Table 2 (Fig. 4). Galatheid crabs, the most abundant associates, were more frequently photographed during the day, as were *Anthias* sp. *H. dactylopterus* may be crepuscular because they were most frequently photographed during early morning and late afternoon (Fig. 4). It is not cer-

[3] Turner, S.C. & B.L. Freeman. Food of tilefish, *Lopholatilus chamaeleonticeps*, unpublished ms.
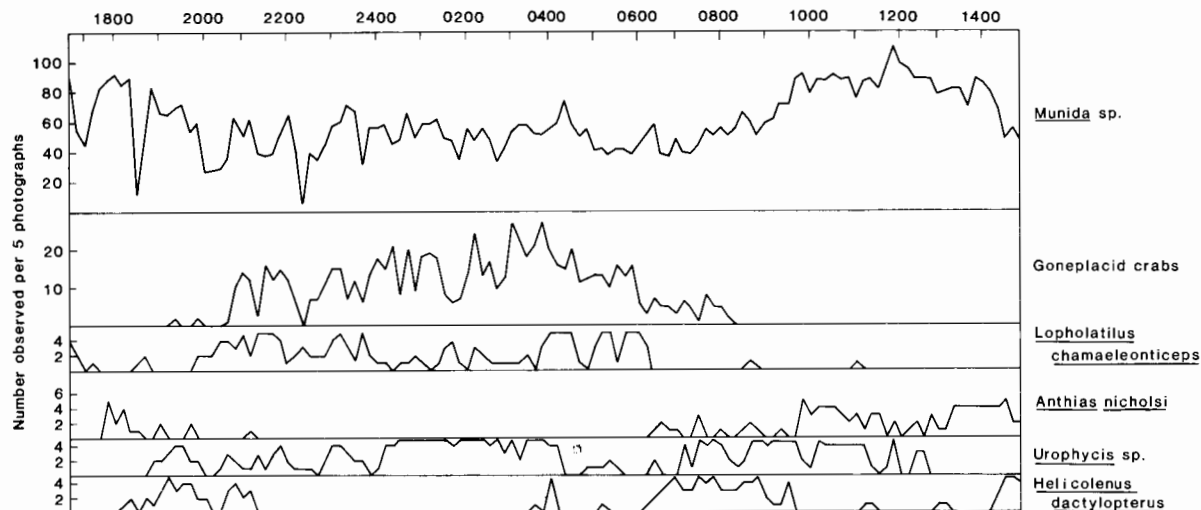
Fig. 4. Temporal activity of tilefish and several associated species at a vertical burrow in Hudson Canyon determined from time lapse photographs.

tain if these animals were responding to available light or avoiding tilefish. The latter seems most likely, at least for *Anthias* sp. and *H. dactylopterus,* because both these species were present well after sunset and before sunrise. Juvenile *Urophycis* sp. activity showed no particular periodicity. Goneplacid crabs were clearly nocturnal, never appearing in photographs exposed after 0810 h and before 1910 h.

Behavior

Tilefish around Hudson Canyon appeared to orient to a particular burrow, and may be longterm residents of the same burrow. Fish observed away from burrows moved quickly, seemingly toward a particular burrow and entered. Rotenone solution was injected into burrows (n = 10) and fish exited slowly tail first after about 1–3 min. However, fish did not leave the proximity of their burrows. They remained in the rotenone solution (opaque and clearly visible) within the burrow cone for several more minutes, or swam out of the rotenone several meters away from the burrow and hovered near bottom. Fish had not been rendered incapable of rapid movement away by the rotenone, because when we attempted to touch them with the submarine manipulator arm they quickly swam away. In one instance a tilefish exited a rotenoned burrow

and attempted to enter a second burrow approximately 2 m away. The fish quickly exited the second burrow (which we subsequently discovered, by rotenone injection, was already occupied by a tilefish) but remained nearby. Longterm residence in a more general area is indicated by mark-recapture data (Grimes et al. 1983 and unpublished data). Twelve tags have been returned from fish at liberty from 115–577 days (five tags were out over one year), and all recaptures were made less than one nautical mile from the release location.

Observations from the submersible have indicated single occupancy of vertical burrows (Able et al. 1982, and we have made many others) however, time-lapse photographs showed a male and a female utilizing the same burrow, and their activity had a definite temporal periodicity (Fig. 4). It was possible to determine the sex of the two fish photographed at the burrow because tilefish are sexually dimorphic, males having larger or more prominent adipose flaps (Katz et al. 1983). We know that the same two fish were repeatedly photographed because of distinguishing body scars. The female was present almost continuously from about 1630 to 2230 h, mostly entering and/or exiting the burrow, and occasionally hovering above or around the burrow. At about 2230 h the male appeared and was observed until 0700 h, usually
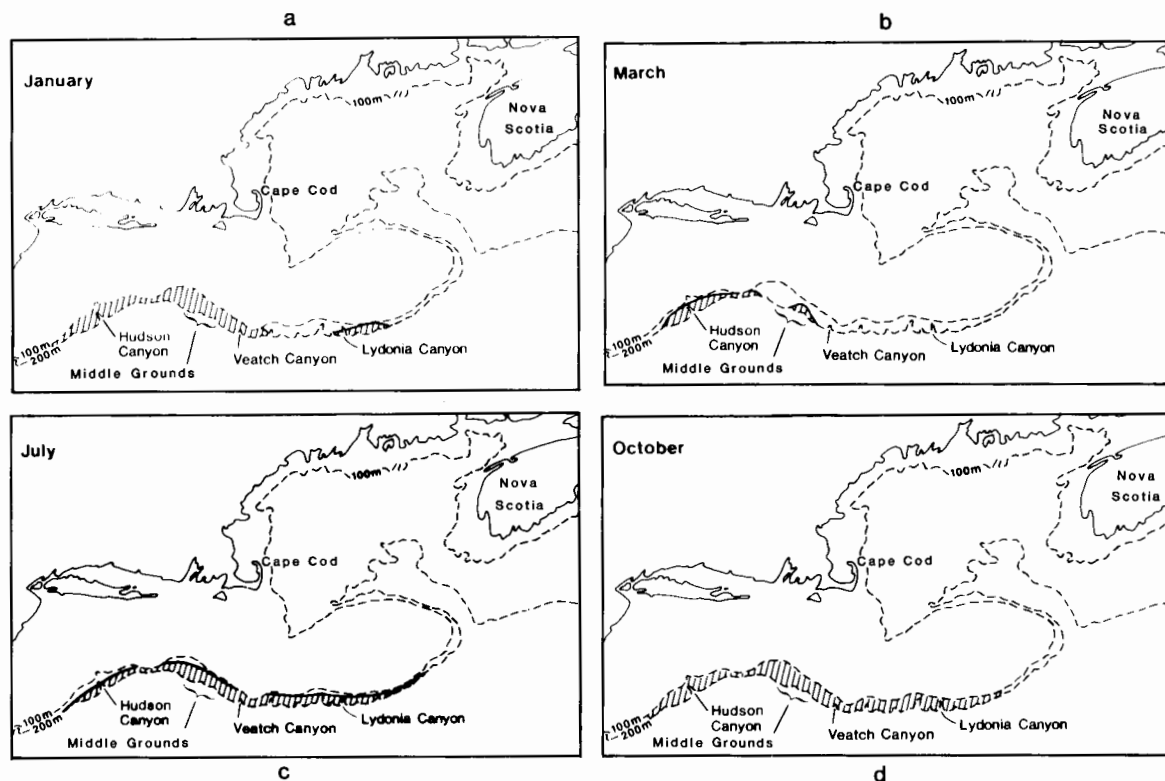
Fig. 5. Mid Atlantic-southern New England continental shelf area between 100–200 m bathed by 9–14° C waters during a representative month for each season.

above the burrow margin or central shaft. We do not know if the female was in the burrow. However, that may be so, because the male was not seen entering or exiting the burrow during that time. From 0700 h until 1500 h only the female was observed near the burrow, in a very few photographs taken between 0900–1000 h and 1100–1200 h. This could suggest that for the most part both sexes were away from the burrow foraging during the day. Diurnal foraging away from burrows by tilefish was suggested by Grimes et al. (1982) because they found a high correlation between tilefish abundance and burrow abundance on submersible transects, but the same relationship was not found during a transect along a baited longline where many more tilefish were seen than would have been predicted from the number of burrows observed.

The non-corresponding temporal activity patterns of some associated species (galatheid crabs,

Anthias sp., *Urophycis* sp. and *H. dactylopterus*) and the knowledge that these species and other associates are common prey of tilefish (Turner & Freeman, unpublished)[1] suggests that predation may be a powerful organizing force in tilefish burrow communities, and probably pueblo habitats as well.

Variation in burrow habitats
We have noted striking burrow variation in degree of secondary burrowing by associates, burrow density (Table 4) and burrow diameter (Table 5) at different dive locations. Burrows at Hudson Canyon and the deep stations (181–243 m) in the Middle Grounds were approximately twice as large (upper diameter), over eight times more dense and much more complex than burrows seen at Lydonia Canyon (Fig. 2f and Tables 4 and 5). Burrows observed approximately 40 nautical miles south of Norfolk Canyon were also smaller (estimated diameter =

0.5–1.5 m, n = 3) and showed less secondary bio-erosion than those seen at Hudson Canyon. Burrows at this site were distinctly less funnel shaped than those at all other sites, and had noticeably greater shaft diameter relative to the upper diameter. The shape difference probably represents a burrow form that is more stable in the softer sediment that burrows were constructed in south of Norfolk Canyon.

We observed burrows over a greater depth range at Hudson Canyon (120–225 m) and the Middle Grounds (102–243 m) than at the two more northern submarine canyons (Veatch Canyon, 120–165 m and Lydonia Canyon, 125–183 m). At Veatch and Lydonia canyons, where boulder and pueblo habitats also occurred, vertical burrows were in shallower water (<183 m, see previous discussion for depths of non-burrow habitats). Burrows observed along the shelf-edge south of Norfolk Canyon occurred between 220–227 m.

In addition to the latitudinal gradients in burrow size, density and complexity, we noted differences in burrow density and size that were correlated with depth at the Middle Grounds. Although we did not make actual measurements, estimated diameter of burrows at the continental shelf-edge (depth = 181–243 m) ranged from 0.5–3.5 m (n = 100), while burrows at shallower stations (depth =

Table 4. Density (mean and range) of tilefish burrows per km² at various dive locations in the Mid Atlantic-southern New England area based on submersible transects; n = number of transects.

Study area	1980	1981	1982	1984	All
Hudson Canyon	1815 (952–2434) n = 4	1239 (1011–1548) n = 2	1132 (592–1646) n = 6	–	1234 (592–2434) n = 12
Veatch Canyon	958 (119–1429) n = 4	772 (748–798) n = 2	–	1531 – n = 1	985 (119–1531) n = 7
Lydonia Canyon	233 n = 1	130 (67–164) n = 2	–	–	145 (67–233) n = 3
Middle Grounds/deep (181–243 m)	–	–	–	1505 (647–2343) n = 8	1505 (647–2343) n = 8
Middle Grounds/shallow (102–134 m)	–	–	–	6300 (2333–10266) n = 2	6300 (2333–10266) n = 2

Table 5. Diameter (mean and range in m) tilefish burrows at various dive locations in the Mid-Atlantic-southern New England area; n = number of burrows measured.

Study area	1980	1981	All
Hudson Canyon	1.57 (0.8–3.5) n = 26	1.60 (0.3–3.0) n = 25	1.60 (0.3–3.5)* n = 51
Veatch Canyon	0.89 (0.4–2.0) n = 20	0.84 (0.3–1.5) n = 20	0.88 (0.3–2.0)* n = 40
Lydonia Canyon	–	0.88 (0.5–1.2) n = 6	0.88 (0.5–1.2) n = 6

* Mean burrow diameters for Hudson and Veatch canyons are significantly different (t = 6.73, $t_{0.05}$ = 1.99).

102–134 m) ranged from 0.3–1.5 m (n = 25). The smaller burrows had little to no secondary bioerosion and were not markedly conical (flaired at the upper margin). Although only two dives were made at shallow stations, it was readily apparent that burrow density was much higher there (approximately 4 times) than at deep Middle Grounds stations (Table 4).

We believe that the differences in burrow habitats within the Mid-Atlantic-southern New England area indicate that burrow habitats in the northeastern part of the study area, and at shallow Middle Grounds stations, are less temporally stable. Reduced habitat stability probably results from greater seasonal variation in bottom temperature in the northeastern and shallower portions of the study area. Longterm (20 yr) average bottom temperature data (Colton & Stoddard 1973) support this interpretation (Fig. 5). The shelf area between 100 and 200 m bathed by relatively warm 9–14° C water has the right combination of temperature and substrate (see subsequent discussion of habitat requirements), and roughly defines the habitable shelf area for tilefish from Georges Bank to just south of Hudson Canyon. Figure 5 shows this area for a representative month for each season, and this area changes with the progression of the seasons. In July, a continuous shelf area from near the east end of Georges Bank to southwest of Hudson Canyon is bathed by the warm waters (Fig. 5c). The maximum shelf area is encompassed in the warm waters in October (Fig. 5d), but the warm area is reduced by winter continental cooling and is absent between Lydonia Canyon and just east of Veatch Canyon in January (Fig. 5a). In March, the shelf area covered by the warm waters is even further reduced, covering only a small area northwest of Veatch Canyon and the Hudson Canyon (Fig. 5b). A large part of the shelf area from around Hudson Canyon to the Middle Grounds, and the small area northwest of Veatch Canyon, are bathed by the warm waters year around (Fig. 5a–d). Note that the reduction in shelf area covered by 9–14° C water proceeds both northeast to southwest (parallel to isobaths) and northwest to southeast (perpendicular to isobaths or shallow to deep). The seasonal reduction in shelf area covered by the warm waters that proceeds from shallow to deep is shown conclusively by bottom temperature data compiled by Chamberlin (1978), Crist & Chamberlin (1978) and Crist & Chamberlin (1979) at about 71° W longitude (the approximate location of the Middle Grounds dives) (Fig. 6).

We speculate that burrows at the more northeastern and shallow Middle Grounds (and less stable with regard to temperature) dive locations are seasonal habitats only occupied at certain times of the year, and that the reduced time of occupancy has resulted in smaller less secondarily bioeroded burrows. In other words, burrows at Lydonia Canyon and shallow Middle Grounds stations are probably only occupied during summer and fall when that area is bathed by 9–14° C water. However, we have made no winter or spring observations to confirm this.

As the temperature data suggests would be possible, the burrows northwest of Veatch Canyon are probably inhabited year around. However, more of the burrows may be occupied in March when fish crowd in from adjacent areas because the 9–14° C water is not present northeast of the Hudson Canyon area except in the area northwest of Veatch Canyon (Fig. 5). Although we have not dived in March to confirm this, our summer observations (proposed period of lower occupancy) and commercial fishery data support our speculations. We found the lowest relative burrow occupancy in summer northwest of Veatch Canyon (50% as compared to 83% and 71% for Lydonia and Hudson Canyon), and commercial longline fishery data showed four to five times greater tilefish abundance (catch-per-unit effort) in March in the area northwest of Veatch Canyon (Grimes et al. 1980, Turner et al. 1983, unpublished).[2]

Around Hudson Canyon and at deep Middle Grounds stations warm temperatures are constant throughout the year, so that the large burrows there are probably occupied year round. That we observed no depth correlated gradient in burrow size and complexity around Hudson Canyon, and that mark-recapture data showed no significant movement for tilefish at liberty up to 577 days (Grimes et al. 1983), are concordant with our interpretation.
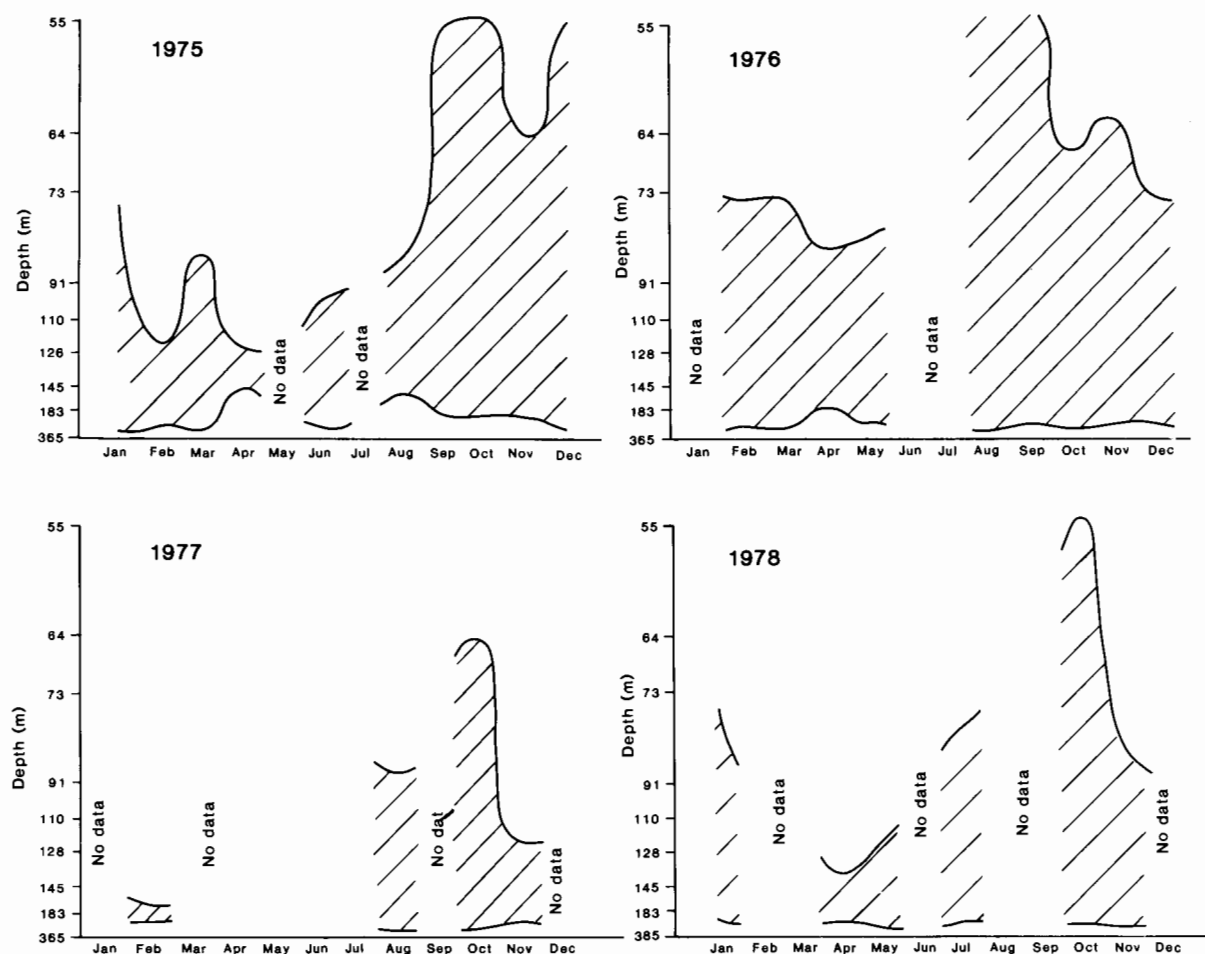
Fig. 6. Seasonal variation in 9–14° C bottom water at 71° W longitude, the approximate location of the Middle Grounds dives. Depth is scaled according to the isobaths at 71° W longitude.

Habitat requirements

There are two critical habitat requirements for tilefish, suitable temperature and shelter. Like others (Dooley 1978, Freeman & Turner 1977), we have always found tilefish associated with a relatively narrow zone of 9–14° C water in the Mid-Atlantic-southern New England region. This 'warm belt' (Verrill 1982) represents the interface between distinct continental slope and continental shelf water masses (Wright 1976). Although the area covered by the warm belt is variable seasonally (Fig. 5, 6) the outer continental shelf and upper slope between 100 and 300 m is frequently bathed in it. Representative temperature and con-

ductivity profiles taken during submersible ascents and descents clearly show the two layered water column, and the warm bottom water where we observed tilefish (Fig. 7). Cooler, but less saline, and thus less dense, continental shelf water rests atop the warmer, but more saline and more dense, continental slope water.

The second requirement, shelter, can be provided by rocks or boulders, or constructed into the substrate in the case of the most important habitats, pueblos and vertical burrows. Able et al. (1982) suggested that clay sediments might be critical to burrow construction, and thus fish distribution. We confirmed this hypothesis using coordinated sidescan sonar, submersible and subbottom
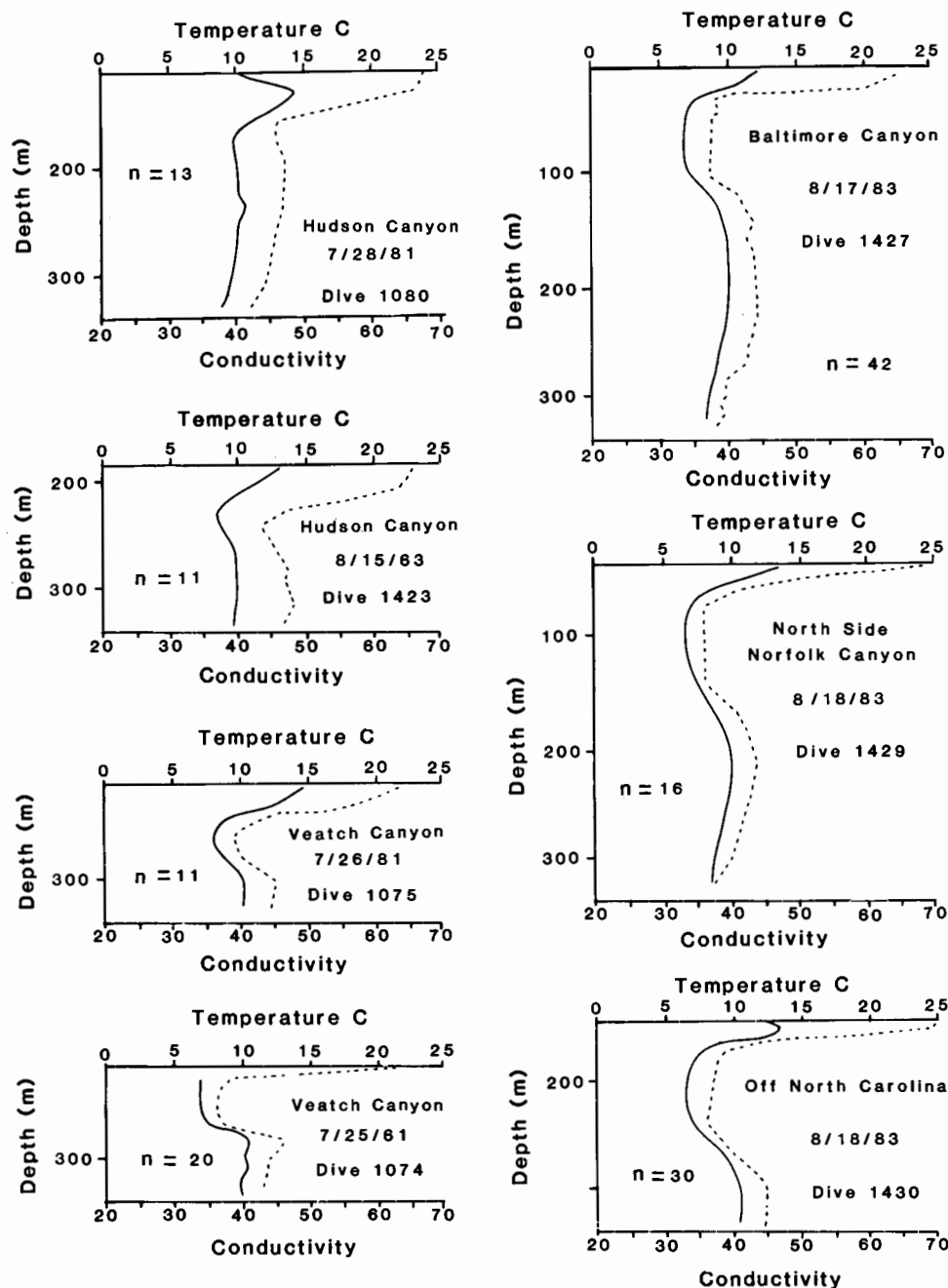
Fig. 7. Temperature (solid lines) and conductivity (broken lines) profiles from dive locations within the Mid Atlantic-southern New England area. N is the number of observations each profile is based upon.

profiling operations. Individual tilefish burrows were identified using sidescan sonar (100 kHz), and a 3.5 kHz depth sounder was used to profile the upper bottom sediments and identify clay. Our interpretation of burrows and clay outcrops seen on sonographs was validated by direct observation during submersible dives (see Twichell et al. 1986 for additional details). In Hudson Canyon and in
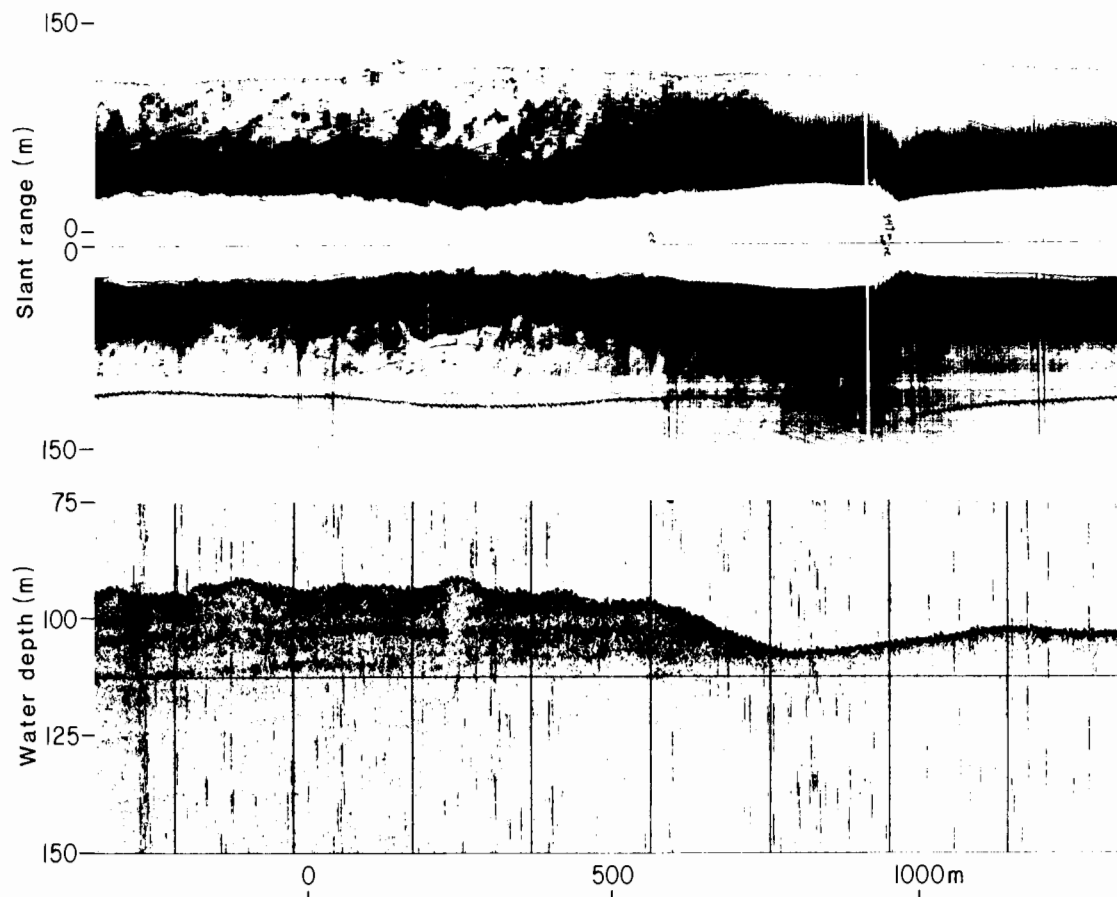
Fig. 8. Sidescan sonogram (upper) and sub-bottom profile (lower) of dive location 1241 on the eastern side of Hudson Canyon showing heavily burrowed and unburrowed bottom. Individual tilefish burrows are points of strong acoustic reflectance and clay sediments are represented by several layers of week acoustic reflectance atop a layer of strong reflectance (sand).

the Middle Grounds burrows were found only where Pleistocene clay sediment was exposed near the substrate surface. For example, at a site along the eastern rim of Hudson Canyon (lat 39° 32.4' N, long 72° 17.5' W) sidescan sonograms and subbottom profiler records indicated a transition from burrowed to smooth bottom and two sediment horizons, a 20 m thick poor acoustic reflecting layer atop a strong acoustic reflecting layer (Fig. 8). Direct visual observations made from the submersible at this site revealed heavily burrowed clay (poor reflecting layer) transitioning to a smooth sand bottom (strong reflecting layer). Across the transition, species composition and water temperature were unchanged.

Tilefish, and their habitats, are particularly abundant around submarine canyons, due to several factors. Around submarine canyons the outer continental shelf and upper slope area between 100 and 300 m is expanded because the isobaths flair where the canyon intersects the continental shelf. This aspect of submarine canyon bathymetry and the right combination of preferred temperature and substrate conditions combine to produce a greater area of suitable bottom for tilefish. Clay is more abundant, exposed, and available for burrowing near canyons due to geologic processes associated with canyons. For example, even though Pleistocene clay sediments are common all along the outer continental shelf and upper slope in the Mid-Atlantic-southern New England area, they are usually not available for burrowing because

they are covered by a sand sheet (Robb et al. 1981). Clay is most abundant around submarine canyons because most continental shelf clay is of deltaic origin, and therefore most common around ancestral river valleys (D.C. Twichell, personal communication). Also, clay is more exposed and available for burrowing around canyons because of active erosional processes (e.g. steeper slopes for slumping and higher current velocities; D.C. Twichell personal communication) and/or the combined effects of past (Pleistocene) erosion and present day non-deposition of sediments (Knebel 1979).

In conclusion, the burrow and pueblo communities are complex ecological systems featuring physical and biological interactions, with tilefish acting as a keystone species (Paine 1966). They shape the habitat and provide a physically suitable environment (and perhaps trophically advantageous as well) for other members of the community. They interact with closely associated small crabs and fishes to further structure and develop the habitat. Finally, they participate in a symbiosis with at least galatheid crabs, and through predation, probably strongly influence community structure.

Acknowledgements

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